

Influence of Changes in Daylength and Carbon Dioxide on the Growth of Potato

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Potatoes (*Solanum tuberosum* L.) are highly productive in mid- to high-latitude areas where photoperiods change significantly throughout the growing season. To study the effects of changes in photoperiod on growth and tuber development of potato cv. Denali, plants were grown for 112 d with $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux (PPF) under a 12-h photoperiod (short days, SD), a 24-h photoperiod (long days, LD), and combinations where plants were moved between the two photoperiods 28, 56, or 84 d after planting. Plants given LD throughout growth received the greatest total daily PPF and produced the greatest tuber yields. At similar levels of total PPF, plants given SD followed by LD yielded greater tuber dry mass (DM) than plants given LD followed by SD. Stem DM per plant, leaf DM, and total plant DM all increased with an increasing proportion of LD and increasing daily PPF, regardless of the daylength sequence. When studies were repeated, but at an enriched ($1000 \mu\text{mol mol}^{-1}$) CO_2 concentration, overall growth trends were similar, with high CO_2 resulting in greater stem length, stem DM, leaf DM, and total plant DM; but high CO_2 did not increase tuber DM.

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INTRODUCTION

Since Garner and Allard's (1923) comprehensive report on photoperiodism in plants, numerous investigators have studied the effects of photoperiod on growth and development of potatoes (*Solanum* spp.) (McClelland, 1928; Werner, 1942; Driver, 1943; Chapman, 1958; Gregory, 1965; Mendoza and Haynes, 1976; Ewing, 1978; Ewing and Wareing, 1978; Batutis and Ewing, 1982; Wheeler and Tibbitts, 1986; Wheeler *et al.*, 1986; Struik, van Huesden and Burger-Meijer, 1988; Wheeler, Tibbitts and Fitzpatrick, 1991). For the most part, these studies have shown that short days (i.e. long nights) promote tuber initiation and growth, while suppressing shoot growth. However, responses have varied depending on species, genotype, and environmental conditions (Gregory, 1965; Mendoza and Haynes, 1976; Ewing, 1985; Wheeler *et al.*, 1986). For example, tuberization will occur in some commercial *Solanum tuberosum* cultivars even under continuous light, if temperatures are kept cool or alternated to provide a thermoperiod (Gregory, 1965; Wheeler and Tibbitts, 1986; Wheeler *et al.*, 1986; Tibbitts, Bennett and Cao, 1990; Wheeler *et al.*, 1991). This suggests that some cultivars are not obligate in their photoperiod requirements, and that the effects of photoperiod can be overridden by other environmental stimuli, such as high irradiance or alternating temperatures (Driver, 1943; Ewing, 1978, 1985; Wheeler *et al.*, 1986, 1991).

In studies where potatoes were grown under changing daylengths, Rasumov (1931) reported that *Solanum demissum* and *Solanum acaule* plants tuberized best when given long days early in growth, followed by short days, suggesting

an obligate requirement for short days for tuberization in these species. However, changes in daylength throughout growth showed little effect on *Solanum tuberosum* cv. Guapa (Rasumov, 1931). Comparisons of several *S. tuberosum* cultivars given either continuously decreasing photoperiods and temperatures ('northern conditions'), or increasing photoperiods and temperatures ('southern conditions') throughout growth showed consistently higher yields from the 'northern' treatment, suggesting that long days followed by short days were also beneficial for some *S. tuberosum* cultivars (Werner, 1942).

Although control of photoperiod on a large scale in the field is impractical, it is easily practised in controlled environments, such as those that might be used for 'seed' tuber production, or closed ecological life support systems (CELSS) proposed for space habitats (Tibbitts, Cao, and Wheeler, 1994). To test whether long days followed by short days, or short days followed by long days, are most favourable for tuber production in potato (*S. tuberosum*), we conducted a controlled environment study in which potato plants were moved between long- and short-day rooms at different stages of development. The study was then repeated, but with enriched CO_2 levels, because evidence from controlled environment studies suggests that benefits of CO_2 enrichment for potato are dependent on both photoperiod and total irradiance (Wheeler *et al.*, 1991).

MATERIALS AND METHODS

All studies were conducted in walk-in (3.7 m × 2.6 m) growth rooms at the University of Wisconsin Biotron. One room was maintained with continuous lighting (long day) and a

second room with a 12-h light, 12-h dark photoperiod (short day). Lighting was provided with cool-white fluorescent lamps and averaged 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux (PPF) at the top of plant canopies. This provided 17.3 $\text{mol m}^{-2} \text{d}^{-1}$ PPF for the short day treatment and 34.6 $\text{mol m}^{-2} \text{d}^{-1}$ PPF for the long day treatment. Air temperatures were maintained at a constant 16 °C (± 0.2 °C) and relative humidity at 70% ($\pm 3\%$), providing a leaf-to-air vapour pressure deficit of 0.5 kPa. Carbon dioxide (CO₂) concentrations in the air were kept near 350 $\mu\text{mol mol}^{-1}$ (i.e. nominal ambient) by continuously supplying fresh air to the room. A second test was initiated 2 weeks following the first, using the same growth rooms, but in this case CO₂ concentrations were enriched to maintain 1000 $\mu\text{mol mol}^{-1}$ by adding pure CO₂ to the incoming air stream.

Potato (*Solanum tuberosum* L. cv Denali) plantlets were propagated *in vitro* (Tibbitts, Cao, and Wheeler, 1994) and transplanted to 38-l pots containing premoistened peat-vermiculite (50:50 v/v). Denali is a high dry matter, late-maturing cultivar, that was chosen because of its tolerance to continuous light, and high yields from controlled environment studies (Wheeler *et al.*, 1991). Plantlets were covered with a glass beaker and one layer of muslin cloth for 72 h to reduce transplant stress, and all pots were watered automatically four times daily with a complete nutrient solution using drip irrigation (Hammer *et al.*, 1978). Fifteen days after planting, an additional 5 cm of peat-vermiculite was added to each pot to bury additional stem nodes to accommodate stolon growth and tuber formation. Pots were placed individually on 72 cm \times 72 cm (cross-sectional area) moveable carts. As plants grew, foliage was confined to the cross-sectional area of the carts by placing support bars between upright posts at each corner of the carts. This provided approx. 0.52 m² area per plant.

Plants were grown for a total of 112 d for each test. At 28, 56, and 84 d after planting, two carts were moved from the short day (SD) room to the long day (LD) room and *vice versa*. In addition, all plants remaining in the rooms were moved to a different position to minimize any position effects. No plants were moved between rooms more than once, and two control plants remained in each room for the duration of the study. Thus separate pairs of plants received one of the following treatments: 28 d SD then 84 d LD; 56 d SD then 56 d LD; 84 d SD then 28 d LD; 112 d SD; 28 d LD then 84 d SD; 56 d LD then 56 d SD; 84 d LD then 28 d SD; or 112 d LD. Because photoperiods were provided with a constant PPF 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, average daily irradiation throughout growth of the different treatments varied as follows: plants receiving only short days—17.3 $\text{mol m}^{-2} \text{d}^{-1}$; plants receiving 84 d SD and 28 d LD—21.6 $\text{mol m}^{-2} \text{d}^{-1}$; plants receiving 56 d SD and 56 d LD—25.9 $\text{mol m}^{-2} \text{d}^{-1}$; plants receiving 84 d LD and 28 d SD—30.2 $\text{mol m}^{-2} \text{d}^{-1}$; and plants receiving 112 d LD—34.6 $\text{mol m}^{-2} \text{d}^{-1}$. Average PPF levels of 21.6, 25.9, and 30.2 $\text{mol m}^{-2} \text{d}^{-1}$ occurred both in LD then SD, and SD then LD treatments, while 17.3 $\text{mol m}^{-2} \text{d}^{-1}$ occurred only with continuous SD and 34.6 $\text{mol m}^{-2} \text{d}^{-1}$ occurred only with continuous LD. At 112 d after planting, all plants were harvested and separated into leaves, stems, roots + stolons, and tubers. The length of the longest stem from each plant was measured. Fresh mass

(FM) of tubers was measured and all other materials were oven dried for at least 48 h to determine dry mass (DM). Tuber DM was determined by drying 300 g of fresh tissue taken from 10 to 12 tubers from each plant and multiplying the percent DM by the total FM. Total dry mass was calculated as the sum of stem, leaf, root + stolon, and tuber dry mass. Harvest index was calculated as [(tuber DM) / (total plant DM)] \times 100.

RESULTS

A comparison of the growth obtained from the various combinations of daylength treatment and CO₂ enrichment is shown in Fig. 1. In general, increasing amounts of PPF and increased CO₂ resulted in increased growth. However, different plant growth interactions resulted with changing light treatments.

Stem length

Stem lengths within each CO₂ treatment showed little difference in response to daylength treatment; i.e. SD then LD plants showed little difference from LD then SD plants, regardless of the average daily PPF (Fig. 1). Increasing the CO₂ from 350 $\mu\text{mol mol}^{-1}$ to 1000 $\mu\text{mol mol}^{-1}$ increased stem length more than 50% at the lowest PPF levels for each daylength sequence, but this effect tended to decrease with increased daily PPF.

Stem dry mass

In contrast to stem lengths, stem DM per plant showed a two- to three-fold increase with increasing PPF, with plants given SD then LD at 25.9 and 30.2 $\text{mol m}^{-2} \text{d}^{-1}$ PPF producing more stem biomass than LD then SD plants (Fig. 1). Stem DM showed nearly a three-fold increase in response to CO₂ enrichment at the lower daily PPF levels.

Leaf dry mass

Leaf DM trends were similar to stem biomass, showing a pronounced increase with increasing daily PPF (Fig. 1). Plants given an average of 30.2 $\text{mol m}^{-2} \text{d}^{-1}$ PPF throughout growth produced more leaf biomass when given SD prior to LD, in comparison to LD prior to SD. There was little difference between plants given SD prior to LD, or LD prior to SD at 21.6 and 25.9 $\text{mol m}^{-2} \text{d}^{-1}$ PPF. Leaf DM was increased from about 40 to 90% by CO₂ enrichment, with the greatest relative increase occurring at the lower PPF levels.

Tuber dry mass

Tuber DM yields were greater from plants that received SD followed by LD for each PPF level (Fig. 1). The greatest tuber DM was obtained from plants given LD and 34.6 $\text{mol m}^{-2} \text{d}^{-1}$ PPF throughout growth. Tuber DM per plant generally showed little response to CO₂ enrichment.

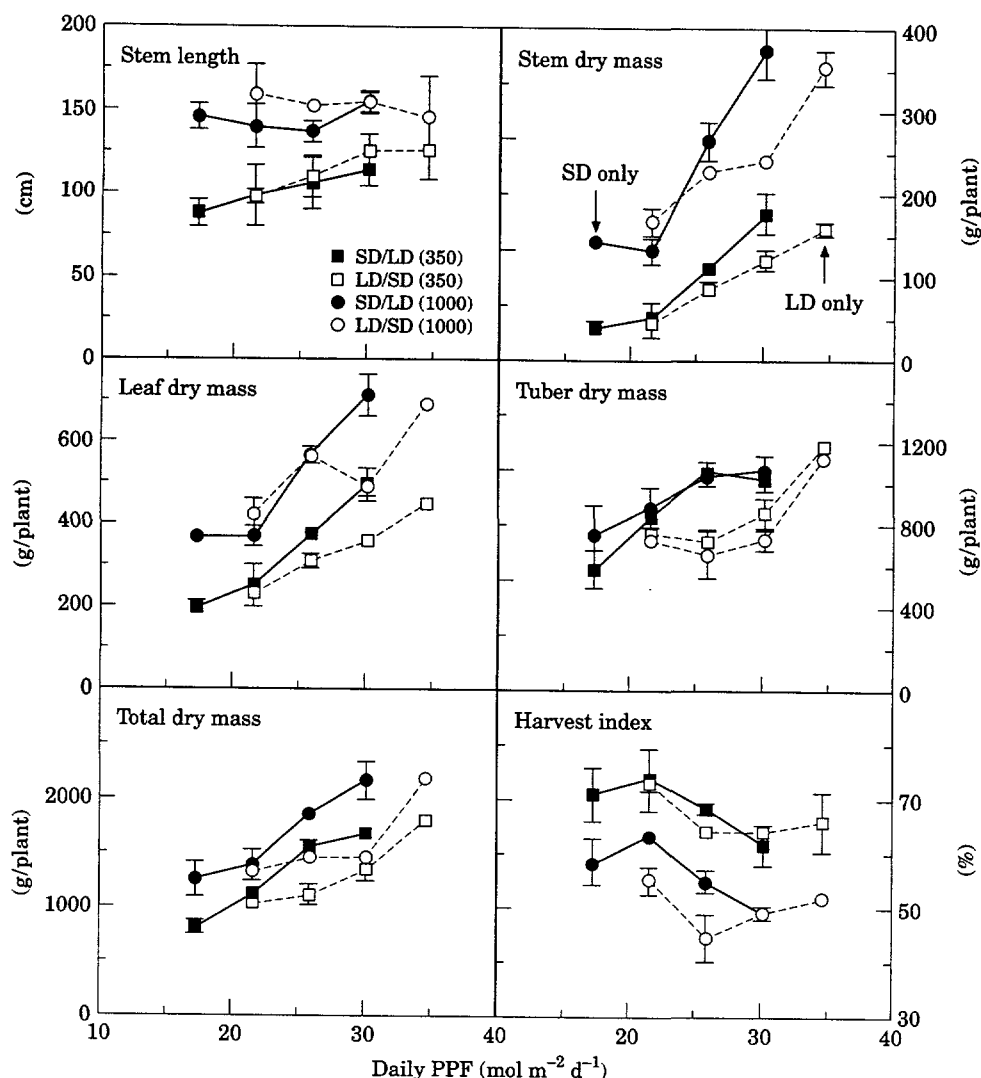


FIG. 1. Effect of daylength sequence on growth of potato cv. Denali. Plants were given short days (SD) only or SD followed by long days (LD) (■ ●), and LD only or LD followed by SD (□ ○). Plants were grown at 350 $\mu\text{mol mol}^{-1}$ CO₂ (■ □) and 1000 $\mu\text{mol mol}^{-1}$ CO₂ (● ○). Lighting treatments were provided with a constant photosynthetic photon flux (PPF) of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with data plotted as a function of average daily PPF provided to the plants throughout the 112-d growth period. Vertical bars indicate s.d.

Roots + stolons

Dry mass of roots and stolons combined, ranged from about 5 to 20 g per plant, for a total of about 1% of the total plant DM. Although most (> 75%) of the root and stolon biomass was recovered and included in total plant DM data, many of the smaller roots could not be separated from the potting medium; thus no comparisons were drawn between treatments.

Total plant dry mass

Plants that received SD prior to LD had greater total plant DM at 25.9 and 30.2 $\text{mol m}^{-2} \text{d}^{-1}$ PPF than plants receiving LD prior to SD, but no difference was apparent from daylength sequence at 21.6 $\text{mol m}^{-2} \text{d}^{-1}$ PPF (Fig. 1). There was an increase in total plant DM with increasing daily PPF. Total plant DM was increased by CO₂ enrichment for all daylength and PPF treatments, with the greatest

relative increase occurring with plants provided SD throughout growth. Total plant DM increased by an average of 24% from CO₂ enrichment for all treatments.

Harvest index

Harvest index tended to decrease with increasing daily PPF, but there were no consistent trends with regard to daylength sequence (Fig. 1). Harvest index was decreased by CO₂ enrichment for all daylength sequences, and the effect did not vary much between daylength treatments or over the range of daily PPF levels.

DISCUSSION

Results from changing the daylength during growth of cv. Denali potato showed that the most favourable sequence for tuber production was SD followed by LD. This finding is not consistent with the observations of Rasumov (1931) and

Werner (1942), who reported that long photoperiods followed by short photoperiods were most conducive for tuber formation. However, both Rasumov's and Werner's studies were conducted in glasshouses where total PPF was probably quite low; in addition, other environmental conditions in these studies were not well documented. More carefully controlled phytotron studies showed little photoperiod response in tetraploid *S. tuberosum* clones when photoperiods were less than 17 h (Mendoza and Haynes, 1976). When *S. tuberosum* cv. Bintje plants were given long days (24 h, with dim light extension) during early development tuber initiation was also delayed, while long days late in development generally delayed tuber growth (Struik *et al.*, 1988).

Results from our study suggest that potatoes grown in the field should do well if planted early in the season when daylengths are short, and then allowed to mature under long days with high PPF. However, temperatures are generally too cold at most mid- to high latitudes settings to start potatoes when daylengths are short (Haverkort, 1990). In mid-latitude settings where temperatures are favourable for early planting, such as California and Israel, yields can indeed be quite high (Horton and Fano, 1985; National Potato Council, 1995). At lower latitudes where fields can be planted much earlier, changes in photoperiod and total irradiance are diminished and the onset of higher temperatures commonly dictates the planting cycles (Haverkort, 1990).

If data are combined for the different daylength and CO₂ treatments in our study, all biomass components showed a near linear increase with increasing average daily PPF. The highest yields for the combined data occurred in the treatment with continuous LD throughout growth, which received the greatest amount of light. This is consistent with findings by Struik *et al.* (1988), who noted high tuber yields in some studies with cv. Bintje plants given long days throughout growth. However, a comparison of tuber yields in the mid-range of PPF levels clearly shows a benefit from having SD before LD (Fig. 1). This suggests that the optimum yields for *S. tuberosum* cvs. selected for high latitudes may be obtained if tuber sinks are initiated by SD early in growth, followed by high daily PPF from LD later in growth to sustain tuber bulking. However, our study only used one cultivar; hence, further studies are needed with other genotypes to confirm this.

Collectively, the evidence suggests that commercial potato (*S. tuberosum*) cvs. grown at mid- to high latitudes have been selected for long critical photoperiods, and that total incident radiation is the most important aspect of lighting to control yield (Driver, 1943; Mendoza and Haynes, 1976; Ewing, 1978; Haverkort, 1990).

Our use of continuous PPF levels for the LD treatment instead of a dim daylength extension or night break, complicates interpretation of true photoperiod effects (Wheeler and Tibbitts, 1986; Struik *et al.*, 1988); but this seemed appropriate for assessing different lighting regimes for potato production in a controlled environment. In production systems which might be used for life support in space, the major constraints will be production time, growing area, and energy requirements (Tibbitts *et al.*,

1994). Thus plant growing systems that have low yields per unit area per unit time may be too costly and, therefore, unacceptable. Plants given SD throughout growth, along with CO₂ enrichment, provided the most efficient energy conversion to tubers, yielding 12.8 g tuber DM m⁻² d⁻¹. By dividing 12.8 g m⁻² d⁻¹/17.3 mol m⁻² d⁻¹, one can estimate that 0.74 g tuber DM were produced per mol of incident radiation. (Note, this does not take side lighting into account, which would tend to inflate radiation conversion estimates.) The greater efficiency resulting from SD throughout, or SD early in growth, supports the tenet that tuberization and/or cessation of shoot growth are short-day responses.

Stem length, stem DM, leaf DM, and total plant DM all showed the greatest relative increase in response to CO₂ at the lowest daily PPF levels (Fig. 1). This runs counter to traditional discussions of limiting factors (Blackman, 1905), but is consistent with the drop in quantum yield and conversion efficiency with increased irradiance (Radmer and Kok, 1977). It is noteworthy that the greatest relative enhancement in total biomass production from CO₂ enrichment occurred in the treatment given continuous SD, where tuber induction and presumably storage sink development would be the strongest. Results from related studies with potato have shown that the greatest proportional increases in total plant and tuber biomass in response to CO₂ enrichment occurred with SD (12 h) *vs.* LD (24 h), and with moderate (400 μmol m⁻² s⁻¹) *vs.* high (800 μmol m⁻² s⁻¹) PPF (Wheeler *et al.*, 1991). CO₂ enrichment showed no significant effect on tuber DM in this study.

We used a constant 16 °C to provide an inductive environment, and this may have diminished the positive effects of CO₂ possible at higher temperatures (Ehleringer and Bjorkman, 1977; Yandell *et al.*, 1988). Diurnal fluctuations in temperature are known to enhance tuberization (Steward, Moreno and Roca, 1981), and related studies with cv. Denali showed that greater tuberization resulted from a 22/14 °C thermoperiod in comparison to a constant 18 °C temperature (Bennett *et al.*, 1991). Hence the responses observed under constant temperatures in this study should be treated with caution when interpreting responses in the field.

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